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STRUCTURAL AND BIOLOGICAL ADAPTATIONS OF VERMETIDAE  
(GASTROPODA) (\*\*)

KEY WORDS: Gastropoda, Vermetidae.

**Abstract**

A review of the structural diversity and adaptive characters of the sedentary gastropods Vermetidae is given.

Modifications of shell, operculum, head-foot and gills are marked.

The methods of food uptake of the microphagous vermetids, ciliary and mucous trap feeding, and also food digestion are characterized.

Reproductive features outlined: fertilization by means of spermatophores, breeding of eggs in mantle cavity, hatching of small juveniles rather than swimming veligers.

Life in aggregations of many vermetids and their role in reef formation pointed out.

Six species of Vermetidae were recorded from the Mediterranean water of Israel, namely: *Vermetus triqueter*, *Vermetus rugulosus*, *Petalconchus glomeratus*, *Serpulorbis arenaria*, *Dendropoma anguliferum* and *Dendropoma petraeum*. Their habitats and structural adaptations treated.

The distribution of these species in the Atlanto-Mediterranean Region indicated.

**Riassunto**

Questo lavoro intende presentare un compendio relativo alla fam. Vermetidae, mettendone in evidenza sia le differenze strutturali sia i caratteri adattativi. Vengono così esaminate le modifiche assunte dalla conchiglia, dall'opercolo, dalla porzione cefalica e dagli ctenidi.

Si prosegue accennando ai sistemi di cattura del cibo da parte dei Vermetidi microfagi, sia ciliare che mediante muco e al susseguente processo digestivo.

Vengono delineati i sistemi riproduttivi: fertilizzazione per mezzo di spermatofori, sviluppo embrionale della uova entro la cavità del mantello. Alla schiusa si hanno più spesso piccoli individui giovanili piuttosto che larve veliger.

Si segnala la vita in forma gregaria di molti Vermetidi e il loro ruolo nella formazione di scogliera coralligene.

Lungo le coste israeliane mediterranee sono state rinvenute sei specie di Vermetidi e precisamente: *Vermetus triqueter*, *Vermetus rugulosus*, *Petalconchus glomeratus*, *Serpulorbis arenaria*, *Dendropoma anguliferum* e *Dendropoma petraeum*, con indicazione dei loro habitat e degli adattamenti strutturali. Viene infine indicata la distribuzione di questa specie nell'areale atlantico-mediterraneo.

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## Introduction

The study of *Vermetidae* was concentrated for many years on features of the shell and operculum. The unusual form of the shell in this sedentary group, in comparison with that of motile gastropods, made their identification very difficult. The first classification of the vermetids by MOERCH (1859-1860) was rather insufficient and distinction of the taxa was often confusing.

A firmly grounded generic classification of the *Vermetidae* has been established by MYRA KEEN (1961). It is based on the coiled pattern of the adult shell, on the protoconch and operculum. This classificatory system is generally accepted today. It paved the way and stimulated work on the functional morphology and anatomy of this odd group of gastropods, to deepen the knowledge of their life processes.

In the last decades a series of publications have appeared dealing with the *Vermetidae*, mainly their biology and ecology: YONGE, 1932; MORTON, 1951, 1955, 1965; HADFIELD, 1970; HADFIELD et al., 1972; HADFIELD & HOPPER, 1980; HUGHES, 1978, 1979; SAFRIEL, 1966, 1974, 1975; SCHEUWIMMER, 1979; HOPPER, 1982 and others. It has been thought useful to review the structural diversity and adaptive characters of *Vermetidae*. This paper is an attempt of a synopsis in this direction. It is based on malacological literature pertinent to this subject, and on observations made on specimens collected in the Mediterranean waters of Israel and in the Gulf of Aquaba.

The *Vermetidae* are sessile gastropods distributed in tropical and subtropical seas (latitude 44°N-44°S), abundant in the intertidal zone and known also in the subtidal zone.

About 50 species of *Vermetidae* are known at present (KEEN, 1961, 1971) belonging to 5 genera: *Vermetus*, *Serpulorbis*, *Tripsycha*, *Petaloconchus* and *Dendropoma*.

Adult vermetids are mostly welded to or imbedded in solid substrate: rocks, stones, coral, shells. The newly hatched juveniles are motile (crawling or also swimming), before they settle on the substrate. The adaptations for the sessile mode of life are reflected in modifications of the shell, operculum, gill, methods of feeding and reproduction.

## The shell

The adult shell lacks the typical spiral snail form: it is tubular and loosely coiled or disjunct. Sculpture is longitudinal or transverse, and often irregular (fig. 1).

The shell of vermetids has convergent resemblance to the shell of sessile tubicolous annelids, such as *Serpulidae*. However the distinction between the shells of these two groups is clear. The *Vermetidae*, like other *Gastropoda*, have a three layered shell, that is glossy inside, and an embryonic spirally coiled shell, whereas the shell of tubicolous annelids is two layered, lustreless within and not spirally coiled from the very beginning.



Fig. 1 - Adult shell of a vermetid (*Serpulorbis*) attached to a shell of *Trochus*.

The shells of *Vermetidae* (*Mesogastropoda*, *Cerithiacea*) have also a confusing similarity to the shells of some other sedentary gastropods: *Siliquariidae* and *Vermiculariidae* (*Mesogastropoda*), *Magilidae* (*Neogastropoda*).

The shells of vermetids are attached to the substrate by their apex.

The apical — nuclear — whorls (2-4) are transparent, colorless, spirally coiled, they are the earliest one of the shell and constitute the protoconch, which appears in the embryo and remains at the apex of the adult shell (fig. 2 e 3). After settling, the adult shell, the teleconch, is built at a right angle to the nuclear whorls. It is irregularly coiled and the last whorls are even disjunct. The aperture is circular. The shell becomes thicker, opaque (due to addition of  $\text{CaCO}_3$ ) and colored, yellow, brown.

The protoconch and the teleoconch are indispensable for identification of the vermetids. It is however a rather hard task to obtain specimens disconnected from their hard substrate without injuring them, especially the nuclear whorls are easily damaged.

In certain vermetids the parts of the shell near the apex are separated by inner septa (\*) from the rest of the shell containing the soft body, e.g. *Serpulorbis* species, *Dendropoma maximum*.

In the shell of *Petaloconchus* calcareous plates (spiral laminae) project and hang down from the upper wall of the tube, their function is unknown.

The shell harbours in its anterior part the relatively small soft body, which is able to retreat wholly into the shell.

## Head-foot

The soft body comprises the head confluent with the foot in front and the visceral mass behind.

The head-foot bears short cephalic tentacles with minute eyes at their outer bases.

The foot, relieved of its locomotory function, is considerably modified and shows specialization associated with the sessile mode of life.

Two long slenderly tapering pedal tentacles (outgrowth of the propodium) flank the opening of pedal gland, they are sensitive exploratory organs, more active than the cephalic tentacles. The mucus secreted by the anterior pedal gland, which opens on the anterior end of the mesopodium (FRETTER, 1962: 111), passes along the pedal tentacles in a narrow longitudinal ciliated tract.

The mucus of the pedal gland is associated in *Vermetidae* with food uptake, whereas in motile gastropods it serves for lubrication of the sole during movement, it is the source of the mucus over which the snail creeps.

The mesopodium is reduced to a small non-creeping sole located between the pedal tentacles. The large posterior part of the foot, the metapodium is truncated plug-like, fitting the aperture of the shell. The outer terminal surface of the metapodium is circular and disc-like. A « horny » spirally wound operculum secreted by the terminal disc is more or less developed and is of various size and shape (fig. 4).

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(\*) The ability to form septa occurs also in the *Turritellidae* and *Caecidae*. These families are included therefore by M. KEEN in the superfamily *Turritellacea*, usually *Vermetidae* are placed in *Cerithiacea*.

The operculum is as wide as the tube, closes completely the orifice of the shell in *Dendropoma*. In *Petaloconchus* and *Vermetus* the operculum is smaller than the aperture. An operculum is lacking in the adult *Serpulorbis*, it appears in its larval stage and is lost at metamorphosis (HUGHES, 1978 b: 121). In *Serpulorbis*, which is non-operculate, the foot is brightly colored (HADFIELD et al., 1972: 94).

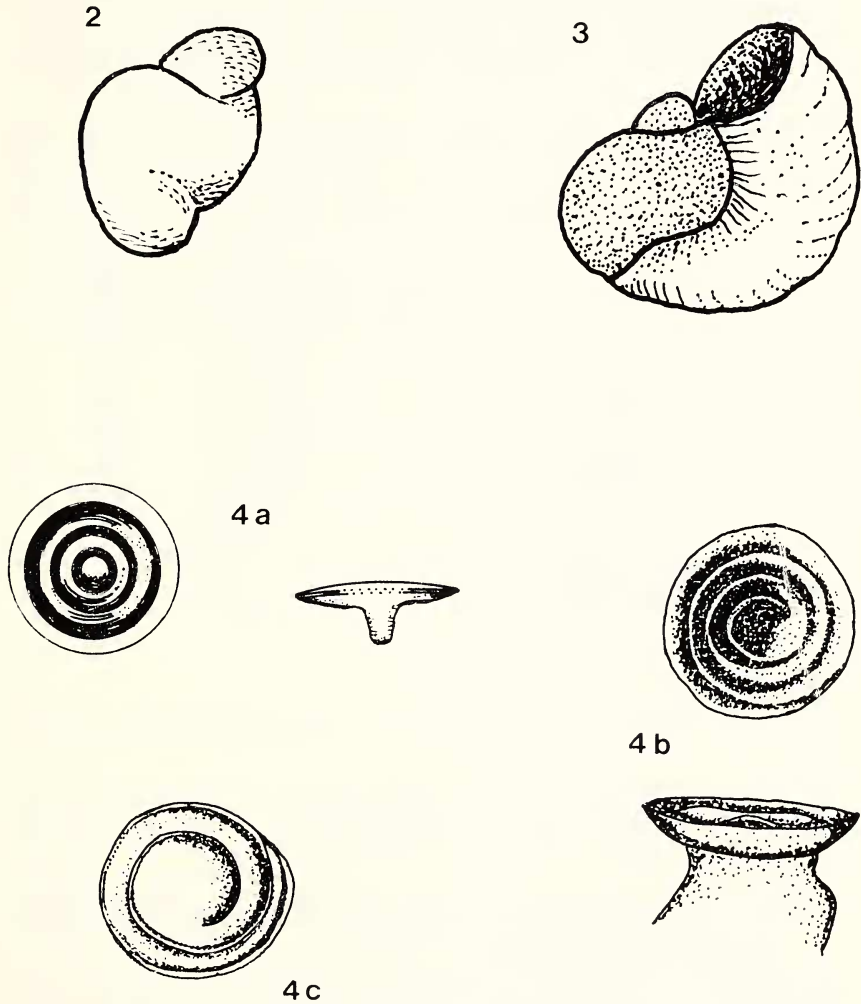


Fig. 2 - Protoconch.

Fig. 3 - Protoconch and initial teleoconch.

Fig. 4 - Opercula (after KEEN): a) operculum of *Dendropoma lamellosum*. Left inner surface, right-side view, showing the mamilla; b) operculum of *Petaloconchus macrophragma*; c) operculum of *Vermetus adansonii*, full view.

The large operculum of *Dendropoma* is pulled by the wide and short columellar muscle against the mouth of the shell and closes it strikingly.

(The anterior end of the columellar muscle is inserted on the underside of the operculum and the posterior end is attached to the shell).

In most *Dendropoma* species the visceral mass is truncated and shortened (MORTON, 1965: 621), and the retreat of the body into the tube is rather slight. The operculum of *Dendropoma* serves thus for effective protection of the animal from wave impact, desiccation in low tide and predators.

Species of vermetids in which the operculum does not close completely the aperture, as *Petaloconchus*, *Vermetus*, or the operculum is lacking as in *Serpulorbis*, the animal protects itself by swift retreat of the body into the earlier whorls of their prolonged shell.

The operculum as well as the protoconch and teleoconch of the shell are necessary for exact identification of the Vermetidae.

### Key to the main genera

1. Operculum present . . . . . 2  
— Operculum absent, foot brightly colored *Serpulorbis* (fig. 6).
2. Diameter of operculum fitting completely the shell aperture; the operculum thick, variable in shape (concave, convex, flat); red or brown in color; inside surface having mostly a distinct central mamilla . . . . . *Dendropoma* (fig. 7 and 4 a)  
— Diameter of operculum smaller than that of the shell aperture; the operculum usually thin, concave . . . . . 3
3. Diameter of operculum at least half diameter of the aperture; spiral laminae (2 or more) projecting from the columellar wall of the shell . . . . . *Petaloconchus* (fig. 4 b).  
— Diameter of operculum less than half diameter of the shell aperture; the small operculum situated on the center of the terminal disc of the foot . . . . . *Vermetus* (fig. 5).

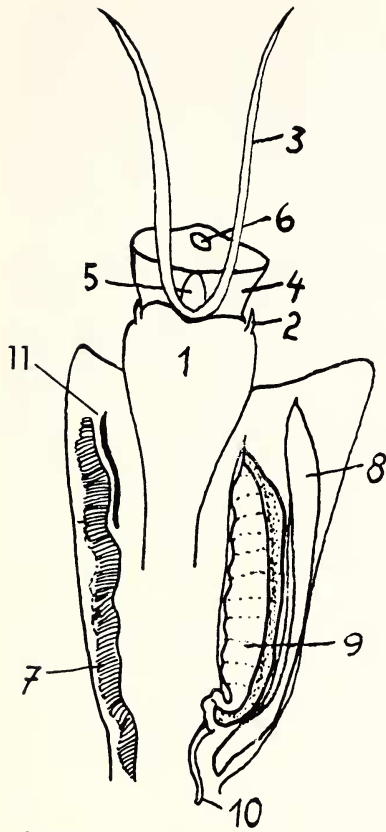


fig. 5

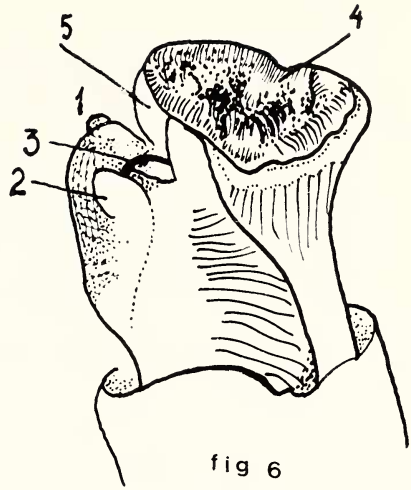


fig 6

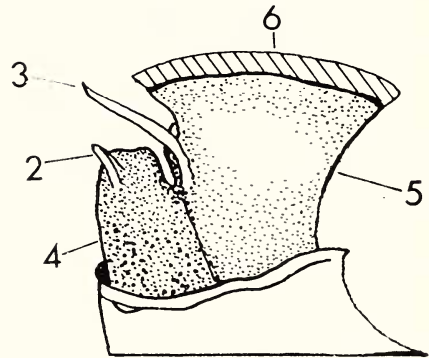


fig. 7

Schemes to morphology of Vermedidae (after MORTON).

Fig. 5 - *Vermetus triqueter*; 1) head; 2) cephalic tentacles; 3) pedal tentacles; 4) foot; 5) sole; 6) operculum; 7) ctenidium; 8) rectum; 9) capsular gland; 10) oviduct; 11) osphradium.

Fig. 6 - *Serpularbis squamigerus*; 1) head; 2) cephalic tentacles; 3) pedal tentacles; 4) foot; 5) sole.

Fig. 7 - *Dendropoma marchadi*; 2) cephalic tentacles; 3) pedal tentacles; 4) head; 5) foot; 6) operculum.

## Respiration

The elongated monopectinate ctenidium is the respiratory organ of the vermetids. It is enclosed in the mantle cavity and extends along it. A series of thin ciliated filaments (leaflets) are attached to one side of the gill axis, which is fused with the left pallial wall.

The filaments are laterally flattened, fixed by their bases to the axis, and hang into the mantle cavity. They are parallelly arranged and water flows freely between them.

The basic form of the filaments is triangular. Their contour may vary from short, comparatively broad-based, equal sized triangles, as in *Serpulorbis variabilis* (HADFIELD et al., 1972: 91), to narrow slender and elongated rods, as in *Vermetus alii* (HADFIELD et al., 1972: 92) (fig. 8).

Long cilia are arranged in rows on the flat surface (lateral) of the leaflets. These cilia generate a current of water flowing through the mantle cavity.

The mantle cavity is divided by the ctenidium into two chambers: the inhalant, on the left, and the exhalant on the right (MORTON, 1951: 8).

Water from outside, drawn by the lateral cilia, enters the inhalant chamber, passes between the gill filaments, and leaves the cavity through the exhalant chamber.

## Feeding

Vermetids feed on particles, such as microscopic plants and animals and detritus.

The proboscis used in capturing food is short, it has two corneous jaws.

The radula is taenioglossate, like in other Cerithioidea, it bears 7 teeth in each row: 1 central, 2 laterals and 4 marginals (2-1-1-2) (fig. 9).

All the teeth, but the central, are erectile, employed in grasping of the food.

Two methods of suspension feeding are known in this family: ciliary (ctenidial) and mucous trap feeding. Most vermetids employ both methods, with predominance of one of them.

In species using primarily the ciliary method, e.g. *Dendropoma petraeum* and *Vermetus alii*, particles suspended in sea water are carried by the inhalant current into the mantle cavity. They are filtered between the mucus covered gill leaflets, mixed there with



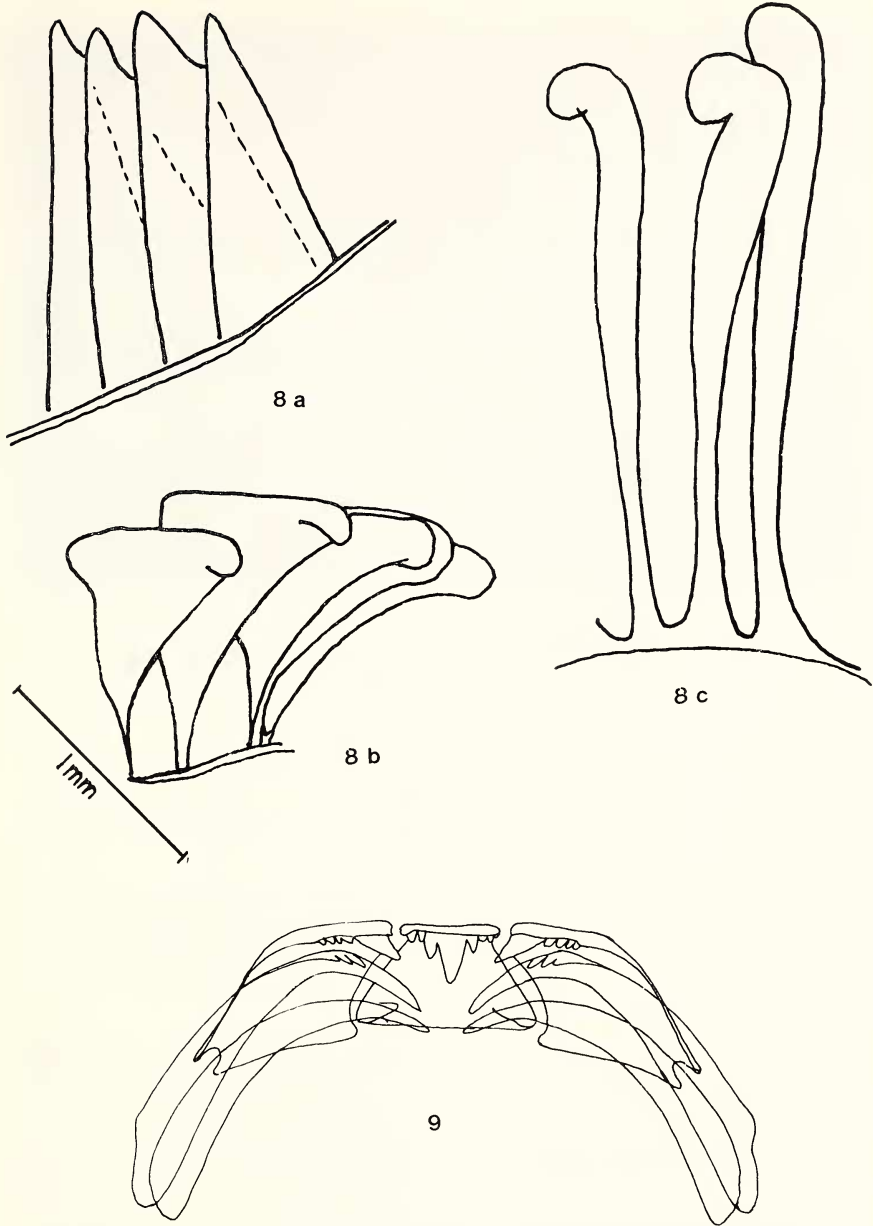


Fig. 8 - Forms of gill filaments (after HADFIELD, 1972): b) triangular lamellae; a) straight-sided triangles; c) club-shaped rods.

Fig. 9 - Taenioglossate radula of Vermetidae.

mucus, and moved forwards in a ciliated tract along the floor of the exhalant chamber. Through a ciliated groove on the right side of the head the particles are led towards the mouth. Mucus from the pedal gland is added to them there, and boluses are formed; they are nipped off by the jaw plates, the radula rakes them into the mouth.

In a typical ciliary feeder the pedal gland is small and the gill filaments are elongated (rod or club-shaped), obviously producing a stronger inhalant water current.

Ciliary feeding is probably best developed in vermetids living in turbulent waters, on surf-beaten surfaces of rocks or raised edges of platforms.

The turbulent water eases ciliary inhaling of water into the mantle cavity and ensures a continuous supply of food. There are however some ciliary feeders living in still water, such as *Vermetus alii* (HADFIELD et al., 1972: 98).

Mucous trap feeders, such as *Serpulorbis arenaria* and *S. natalensis*, capture food particles by means of mucous threads interlaced to form sheets or nets. The threads are formed from droplets of mucus extruded from the pedal gland, their length may reach up to 40 cm. The threads are spun in the ciliated grooves of the pedal tentacles; they are held at the site of their origin, the opening of the mucous gland. Food particles stick to the mucous trap spread into the water, the increased catch area of the trap is obviously efficient for the collection of food. From time to time the trap is hauled towards the mouth by the radula.

Predominantly mucous feeders, such as *Serpulorbis arenaria* and *Vermetus triqueter* are common in calm waters (beneath rocks, in sheltered pools), the mucous trap hangs here undisturbed while gathering food material (fig. 10).

However, certain mucous feeders, e.g. *Dendropoma irregulare* (SAFRIEL, 1975: 97), *Serpulorbis variabilis*, *Petalonchus montereyensis* (HADFIELD pers. com.) occur in rough waters. *Dendropoma corallicinum* occurs on all exposed rocky shores, but is never found in very sheltered situation (HUGHES, 1978 b: 112).

Certain features are characteristic of typical mucous feeders: the pedal gland is large and the pedal tentacles are long. The gill leaflets are short and triangular (in correlation with their minor function in food supply). The operculum is usually small (*Vermetus*) or lacking (*Serpulorbis*). The presence of a developed operculum might impede the employment of mucous strings, because the mucous threads attached to the edges of the shell would be torn when

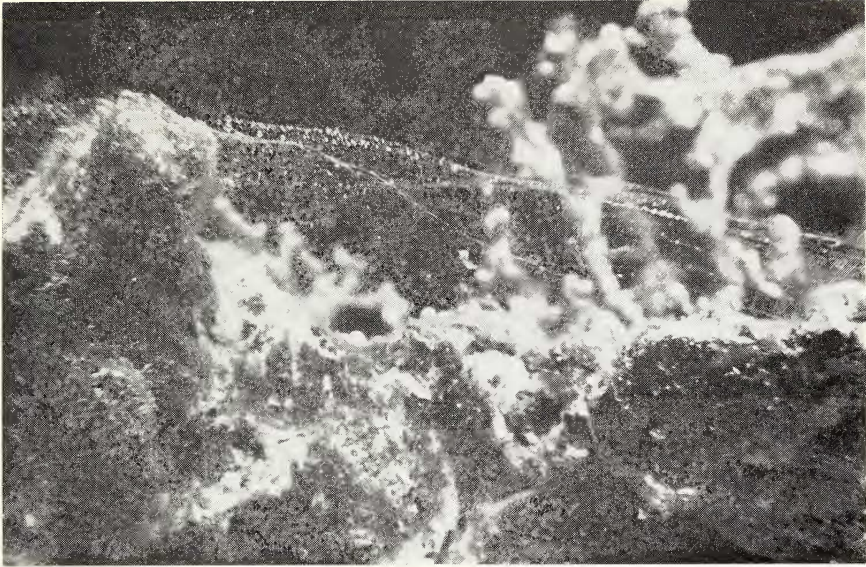


Fig. 10 - Mucous feeding net of *Serpulorbis* sp. (in aquarium).

the animal withdraws into the shell (MORTON, 1955). However, *Dendropoma maximum* (the largest vermetid of tropical Pacific waters) and *Dendropoma corallinaceum* having large opercula, feed predominantly by mucous net (HUGHES, 1978 b; HUGHES & LEWIS, 1974; HADFIELD pers. com.).

The terminal part of the shell is often upturned vertically, raised above the substrate, where mucous threads may be less disturbed by water currents produced by other organisms on the substrate (Sponges, Bryozoa).

For instance: the distal part of the shell of *Serpulorbis inopertus*, common in the reef zone of Aquaba among algae, is raised up to 3-6 cm above the level of the other whorls (MASTELLER, 1979: 293).

Similarly are raised the orifices of the shells of *Serpulorbis aureus* (HUGHES, 1978 a: 289).

Ciliary feeding occurs also in other prosobranchs, such as *Turritella*, *Calyptraea* and *Capulus*. This method seems to be the original one also in vermetids. The mucous trap feeding is a peculiar trait of Vermetidae only.

An additional way of feeding by grazing was also observed by HOPPER (1982: 38). « Individuals of *Dendropoma gregaria* are capable of grazing the substratum around their aperture and they will eat any algal or animal detritus within reach of their aperture. The animal extends its head and neck several millimeters beyond the edge of the shell aperture and grasps detritus with the jaws or rasps the substratum with the radula ».

#### Predominantly mucous feeders

Species	Authorities
<i>Vermetus triqueter</i>	MORTON, 1965: 618
<i>Serpulorbis arenaria</i>	MORTON, 1965: 618
<i>Serpulorbis natalensis</i>	HUGHES, 1978-b: 121
<i>Serpularbis squamigerus</i>	HADFIELD et al., 1970: 305
<i>Serpulorbis variabilis</i>	HADFIELD et al., 1972: 91
<i>Tripsycha tulipa</i>	HUGHES, 1982 (pers. com.)
<i>Petalococonchus montereyensis</i>	HADFIELD, 1970: 307
<i>Petalococonchus nigricans</i>	MORTON, 1965: 618
<i>Dendropoma corallinaceum</i>	HUGHES, 1978-b: 121
<i>Dendropoma irregulare</i>	SAFRIEL, 1974: 1115
<i>Dendropoma maximum</i> (*)	HUGHES & LEWIS, 1974: 544
<i>Dendropoma rhyssococoncha</i>	HADFIELD et al., 1972: 89
<i>Dendropoma corrodens</i>	ABBOTT, 1974: 100

#### Predominantly ciliary feeders

Species	Authorities
<i>Vermetus alii</i>	HADFIELD et al., 1972: 94
<i>Serpulorbis novaehollandiae</i>	MORTON, 1951: 11
<i>Serpulorbis zelandicus</i>	MORTON, 1951: 11
<i>Dendropoma lamellosa</i>	MORTON, 1965: 618
<i>Dendropoma petraeum</i>	SAFRIEL, 1975: 97

Digestion is confined to the complex stomach and to the digestive gland.

The food particles ingested into the buccal cavity are brought through the ciliated oesophagus into the ovoid stomach. In the stomach of *Serpulorbis inopertus* were found fine particles of sediment, Chrysophyceae, fragments of filamentous green algae, diatoms and planktonic crustacean larvae (MASTALLER, 1979: 283).

(\*) *Dendropoma maximum* was indicated by MORTON (1965: 618) as an entirely ciliary feeder, relying on YONGE (1932). The mucus secreting pedal gland was found to be smaller in *D. maximum* and its gill filaments much larger than those of other vermetids. According to HUGHES et LEWIS (1974: 544) *D. maximum* has been found to feed continuously from mucous net.

The walls of the proximal globular region of the stomach are characterised by a ciliated sorting area of grooves and ridges (HYMAN, 1967: 223).

The food is stirred by muscular contractions of the stomach walls; finer particles are drawn into the paired ducts of the digestive gland, which opens into the stomach, larger and heavier particles are directed by the sorting area towards the intestine for rejection.

The food, while in the gastric cavity, is subjected to an initial extracellular digestion. The main source of the digestive enzymes there is the crystalline style (\*), a firm mucous rod secreted in a caecal pouch of the stomach, the style sac (OWEN, 1966: 56). The crystalline style protrudes from the style sac into the stomach and is rotated continuously by cilia of the sac wall. The style is impregnated by several carbohydrate breaking enzymes (amylases and glycogenases) (HYMAN, 1967: 397).

The free end of the style rubs against the gastric shield (MORTON, 1951: 12), a cuticular plate in the stomach wall. This abrasive action liberates enzymes into the stomach.

Digestion is thus in part extracellular (stomach) and partially intracellular (SALVINI-PLAWEN, 1981: 391). The intracellular process of digestion proceeds within the mid-gut digestive gland, which consists of numerous blind-ending tubules communicating with the stomach by a system of branched ducts. Digestion takes place in the walls of the tubules by digestive enzymes (proteolytic and others). Particles not digested in the tubules pass back by beating of cilia to the stomach and thence to the long looped intestine.

Faeces are primarily formed in the intestine; the waste particles are aggregated by mucus, and after consolidation firm faecal pellets are formed (fig. 11). They are accumulated in rows in the wider rectum, which opens by the anus near the outer edge of the mantle (MORTON, 1965: 591, fig. 3 A). The pellets are rejected and swept away by the exhalant pallial current.

Vermetids living in dense aggregations, as many species of *Dendropoma*, are likely to become contaminated by accumulation of faeces in the surrounding water. Pollution is presumably prevented by the turbulence of the water in which these species are found.

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(\*) A crystalline style is present in the gut of bivalves and certain micro-herbivorous gastropods belonging to Mesogastropoda. It occurs in the super-families Stromboidea (*Aporrhais*, *Lambis*), Calyptraeoidae, Rissoidea and a few families in Cerithioidea e.g. Turritellidae, Melaniidae, Cerithiidae (FRETTER & GRAHM, 1962; OWEN, 1966; HYMAN, 1967; HOUBRICK, 1978). Occurrence of a crystalline style in Neogastropoda is rare, perhaps unique in Nassariidae, e.g. *Ilyanassa obsoleta*.



Fig. 11 - Pellets of *Dendropoma cf. meroclista*.

## Reproduction

The sexes are separate in vermetids. The single gonad (testis or ovary) is lodged in the visceral mass. The male lacks a copulatory organ, as other Cerithioidea. Fertilisation is internal, which is characteristic for mesogastropods and neogastropods (HYMAN, 1967: 301).

The sperm are enclosed in spermatophores (fig. 12), produced within the male gonoduct. The spermatophores are pelagic (\*), they are liberated by the male into the sea water, dispersed by waves and currents, and chance to reach the female. Observations on the structure of spermatophores and the discharge of spermatozoa from them

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(\*) The production of pelagic spermatophores has been reported in sessile tubicolous marine invertebrates belonging to Pogonophora (IVANOV, 1960: 1588); Phoronida, Polychaeta, some Chaetopteridae and Spionidae (HADFIELD & HOPPER, 1980: 315), and Syllidae (LIVANOV, 1947: 69).

Spermatophores produced in other groups, e.g. Cephalopoda, Copepoda, Insecta and Urodela, are mostly transferred directly into or onto the female.

were made by SHEUWIMMER (1979) on *Serpulorbis imbricatus*, and by HADFIELD & HOPPER (1980) on species of three genera: *Serpulorbis variabilis*, *S. squamigerus*, *Petalococonchus montereyensis*, *Dendropoma gregaria*, *D. platypus*, *D. psarocephala* and *D. rhysoconcha*.

The vermetid spermatophores are oval to tear-drop shaped, their length ranging from less than 1 mm to 12,5 mm. The opaque sperm mass (yellow to brown) lies within a sperm sac drawn into a narrow coiled ejaculatory tube. The sperm sac is surrounded by 3 membranes. The membrane nearest to the sperm sac — the primary membrane — lies close to the secondary membrane; sometimes they coalesce to form one, as in *Petalococonchus montereyensis*. The tertiary membrane, the external one, is separated by fluid from the secondary. The external membrane is often drawn out into filaments at each end of the spermatophore.

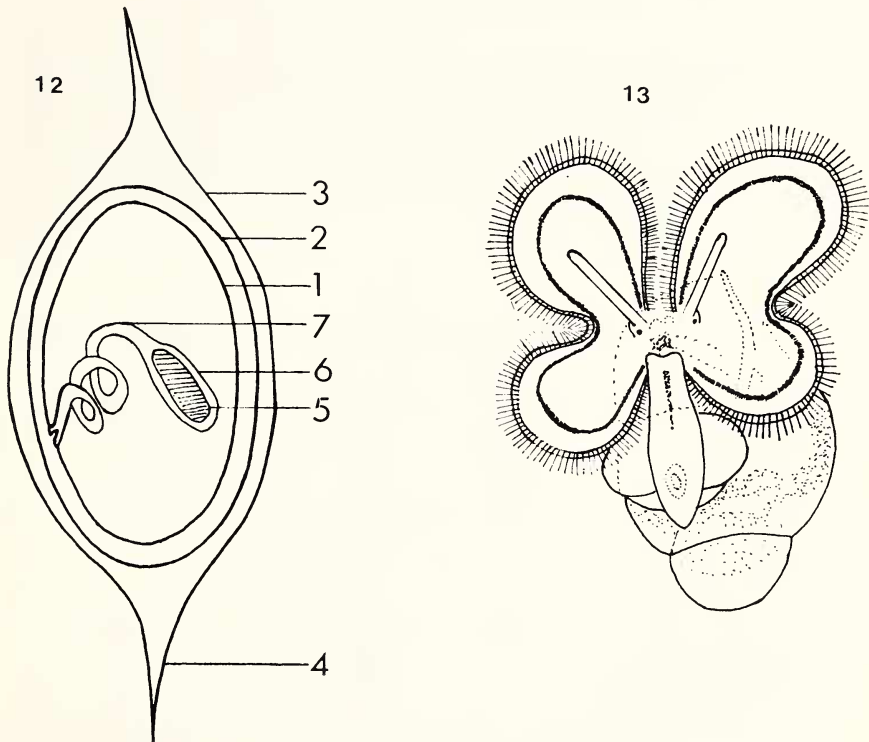


Fig. 12 - Diagram of vermetid spermatophore (after HADFIELD & HOPPER, 1980): 1) primary membrane; 2) secondary membrane; 3) tertiary (external) membrane; 4) end filament of external membrane; 5) sperm mass; 6) sperm sac; 7) ejaculatory tube.

Fig. 13 - Advanced stage of veliger (*Serpulorbis imbricata*) at hatching (after HABE, 1953). Velum bilobed.

When spermatophores are drifted by the inhalant current or caught in mucous feeding nets, they are brought to the mouth of the female. There the walls of the spermatophores are ruptured by pressure of the jaws and radula. The sperm sac is liberated and brought into the pallial cavity by inhalant current. The ejaculatory tube of the sac everts and uncoils, and the process of pouring out of sperm from the sperm sac begins. The released spermatozoa are obviously carried to the female gonopore by the beating cilia in the oviduct. They are stored in the pouch-like receptaculum seminis, where they remain viable until fertilization of the eggs.

The vermetids produce dimorphic sperm: small eupyrene (typical spermatozoa) and larger apyrene (atypical) spermatozoa. The latter are incapable of fertilizing eggs. The apyrene spermatozoa disintegrate within the female genital apparatus or within the male gonoduct. It is assumed that the apyrene spermatozoa serve as nutrient for the typical spermatozoa (SCHEUWIMMER, 1979).

The eggs are fertilized in the proximal portion of the oviduct, near the receptaculum seminis. After fertilization the eggs are embedded in a fluid secreted by the albuminous gland associated with the oviduct. Groups of eggs are enclosed in thin-walled transparent capsules. The number of capsules and the number of eggs per capsule varies in the species:

Species	No. of capsules	No. of eggs per capsule	Authorities
<i>Vermetus alii</i>	50	80-220	HADFIELD et al., 1972: 97
<i>Vermetus triqueter</i>	4-6	85-115	BANDEL, 1975: 90
<i>Serpulorbis imbricatus</i>	20-30	70-80	HABE, 1953: 161
<i>Serpulorbis variabilis</i>	48	240	HADFIELD et al., 1972: 97
<i>Petalococonchus erectus</i>	?	over 100	BANDEL, 1976: 258
<i>Petalococonchus keena</i>	5	130-184	HADFIELD et al., 1972: 97
<i>Petalococonchus mcgintyi</i>	3-4	80-100	BANDEL, 1976: 257
<i>Dendropoma maximum</i>	11	335	HUGHES & LEWIS, 1974: 547
<i>Dendropoma meroclista</i>	3-6	3-16	HADFIELD et al., 1972: 97
<i>Dendropoma gregaria</i>	3-4	6-21	HADFIELD et al., 1972: 84
<i>Dendropoma platypus</i>	5	24-70	HADFIELD et al., 1972: 97
<i>Dendropoma rhysoconcha</i>	6	6-25	HADFIELD et al., 1972: 97
<i>Dendropoma psarocephala</i>	5	9-23	HADFIELD et al., 1972: 97

The soft wall of the capsule is secreted by the capsular gland which makes up the distal part of the pallial oviduct. The egg capsules are discharged through the opening of the gonoduct into the pallial cavity and kept there for brood protection.



The Vermetids exhibit two methods of brooding:

1. The egg capsules lie free in the mantle cavity.
2. The egg capsules are attached by stalks to the inner surface of the shell roof (MORTON, 1965: 609, fig. 11 B).

There is a dorsal medium slit in the mantle of the female under the shell roof, through which the egg capsules pass to hang suspended in the mantle cavity (HUGHES & LEWIS, 1974, plate 1 b: 538).

The methods of brooding bear no strict relation to taxonomy and cannot be considered as a general character of taxa at the generic level.

Egg capsules lie mostly free in the mantle cavity in *Dendropoma* and *Petalococonchus*, and the mantle of the female is entire. However, there are species of these genera in which the egg capsules are attached to the roof of the shell, e.g. *Dendropoma maximum*, *Dendropoma meroclista* and *Petalococonchus keenae*. The egg capsules are usually attached to the roof of the shell in *Serpulorbis* and *Vermetus*, but in *Vermetus alii* the egg capsules lie free and the mantle is entire in both sexes (HADFIELD et al., 1972).

It is noteworthy that species in which the egg capsules are lying free in the mantle cavity belong mostly to species of *Dendropoma* that have a developed operculum closing the aperture of the shell and the protection of the brood is thus more or less efficient.

The retreat of the soft body is slight and there is no risk of crushing the eggs sheltered in the mantle cavity.

Species in which the egg capsules are attached to the shell belong mostly to genera in which the operculum is reduced (*Vermetus*) or is completely lacking (*Serpulorbis*). When disturbed these animals retreat deeply into the shell. Due to the pallial slit in the female, the mantle glides back, leaving the egg capsules fastened to the shell wall anteriorly.

The capsules lie free in the mantle cavity

Species	Authority
<i>Dendropoma corallinaceum</i>	HUGHES, 1978 b: 125, fig. I-A
<i>Dendropoma gregaria</i>	HADFIELD et al., 1972: 82
<i>Dendropoma irregulare</i>	MORTON, 1965: 597, fig. 4-c
<i>Dendropoma marchadi</i>	MORTON, 1965: 597, fig. 1-a
<i>Dendropoma platypus</i>	HADFIELD et al., 1972: 84
<i>Dendropoma psarocephala</i>	HADFIELD et al., 1972: 85
<i>Dendropoma rhyssococoncha</i>	HADFIELD et al., 1972: 89
<i>Dendropoma tholia</i>	MORTON, 1965: 597
<i>Petalococonchus montereyensis</i>	MORTON, 1965: 600, fig. 6-c

The capsules attached to the roof of the shell (pallial slit in female)

Species	Authorities
<i>Dendropoma maximum</i>	HUGHES & LEWIS, 1974: 543, fig. b, plate I
<i>Dendropoma meroclista</i>	HADFIELD et al., 1972: 84
<i>Petalococonchus erectus</i>	BANDEL, 1976: 257
<i>Petalococonchus keenae</i>	HADFIELD et al., 1972: 90
<i>Petalococonchus mcgintyi</i>	BANDEL, 1976: 257
<i>Vermetus triqueter</i>	MORTON, 1965: 609, fig. 11-b
<i>Serpulorbis aureus</i>	HUGHES, 1978 a: 288, fig. 2-c
<i>Serpulorbis imbricatus</i>	HABE, 1953: 161-162
<i>Serpulorbis natalensis</i>	HUGHES, 1978 b: 125, fig. 8-A
<i>Serpulorbis squamigerus</i>	HADFIELD, 1970: 303, fig. 4, plate 45
<i>Serpulorbis variabilis</i>	HADFIELD et al., 1972: 91
<i>Serpulorbis zelandicus</i>	MORTON, 1951: 16
<i>Serpulorbis medusae</i>	SCHEUWIMMER & NISHIWAKI, 1982: 95
<i>Serpulorbis daidai</i>	SCHEUWIMMER & NISHIWAKI, 1982: 93

The embryonic development is completed within the investments of the egg.

The larvae move about in the fluid of the capsule before hatching.

When the capsular wall is ruptured (probably by the sharp edge of the embryonic operculum), the larvae are released.

The forms and size of the hatching larvae are correlated with the amount of food available to the embryos in the egg capsule. The food comprises the yolk in the ova and the nutrients (albumen) in the capsular fluid.

In some species, such as *Petalococonchus keenae*, *P. erectus*, there is an additional source of food within the capsule - nurse eggs. These eggs fail to undergo normal development and they are devoured by the embryos.

Embryos with a small supply of nutrients hatch as swimming larvae-veligers. Only in a few species are larvae released in veliger stage to swim free in the sea.

Veliger larvae appear, for instance, in *Serpulorbis variabilis*, *S. imbricatus*, *Vermetus alii*. For example: veligers of *Serpulorbis imbricatus* are small, 0.44-0.63 mm. The shell on the posterior part of the body is thin, yellow, consisting at hatching 3½ whorls. At the anterior end of the body a bilobed ciliated velum provided with a pair of minute tentacles, a minute eye at the base of each tentacle. An otocyst is at the base of the small foot. The foot carries a minute operculum (HABE, 1953: 161) (fig. 13).

## Larval stages after hatching observed in Vermetidae

Species	Veliger	Veliconcha	Crawling	Authorities
<i>Vermetus alii</i>	+			HADFIELD et al., 1972: 94
<i>Vermetus triqueter</i>		+	+	BANDEL, 1975: 90
<i>Serpulorbis aotearoicus</i>			+	MORTON, 1951: 15, fig. 22
<i>Serpulorbis aureus</i>			+	HUGHES, 1978 a: 288, fig. 2
<i>Serpulorbis imbricatus</i>	+			MORTON, 1965: 613
<i>Serpulorbis natalensis</i>			+	HUGHES, 1978 b: 120, fig. 8
<i>Serpulorbis zelandicus</i>			+	MORTON, 1951: 15
<i>Serpulorbis variabilis</i>	+			HADFIELD et al., 1972: 92
<i>Petalococonchus erectus</i>		+		BANDEL, 1976: 258
<i>Petalococonchus keenae</i>	rarely		+	HADFIELD et al., 1972: 90
<i>Petalococonchus mcgintyi</i>	+			BANDEL, 1976: 257
<i>Petalococonchus nigricans</i>	+			MORTON, 1965: 613
<i>Dendropoma corallinaceum</i>			+	HUGHES, 1978 b: 117, fig. 4
<i>Dendropoma gregaria</i>			+	HADFIELD et al., 1972: 83
<i>Dendropoma maximum</i>			+	HUGHES et LEWIS, 1974: 543
<i>Dendropoma meroclista</i>	occasionally		+	HADFIELD et al., 1972: 84
<i>Dendropoma platypus</i>	rarely		+	HADFIELD et al., 1972: 86
<i>Dendropoma psarocephala</i>			+	HADFIELD et al., 1972: 86
<i>Dendropoma rhyssococoncha</i>			+	HADFIELD et al., 1972: 89

The veligers are able to swim by means of their velum and they are carried by waves and currents. They remain in the plankton from few hours to several weeks. As metamorphosis proceeds, the velum degenerates and is reabsorbed. The foot is transformed to allow creeping, the larvae leave the plankton and become benthos dwellers in crawling stage.

Most vermetids hatch in crawling stage. Crawling juveniles hatch from eggs containing a large amount of food. They morphologically resemble the adults of errant prosobranchs. Their foot is developed and they are able to creep about and grip hard surfaces. The cephalic tentacles are long at this stage and the juveniles carry a minute spiral shell (protoconch) on their dorsal side. The propodium occupies the tip of the foot, on its corners are small protuberances - the rudiments of the pedal tentacles. The foot is dominated by the mesopodial surface (sole). The metapodium carries the operculum.

The crawling stage lasts for a limited time, e.g. 1-4 days in *Dendropoma corallinaceum* (HUGHES, 1979 b: 425), 1-5 days in *Dendropoma gregaria* (HOPPER, 1982: 221). When the crawling juveniles are about to settle, their body undergoes considerable changes: the juvenile spiral shell becomes attached to the substrate by a calcareous « cement », secreted from the pedal gland, and the irregular shell of

the adult begins to develop (HOPPER, 1982: 185, fig. 31). With the attachment the corners of the propodium elongate to form highly motile pedal tentacles, longer than the cephalic tentacles.

The mesopodium is reduced to a fold of tissue (remnant of the sole).

The metapodium is truncated, plug-like, it becomes the major portion of the foot, it either bears an operculum or an operculum is wanting (*Serpulorbis*).

In some species from eggs with a considerable amount of food hatch larvae veliconchae, as in *Vermetus triqueter* (BANDEL, 1975: 90), *Petalococonchus erectus* (BANDEL, 1976: 258). These larvae are able to swim heavily for some hours and also to move by creeping. After a short time in plankton they sink to the substrate and complete the metamorphosis.

In *Dendropoma* after settlement the young snail erodes by the radula a groove in the substrate. Calcareous substrates or surfaces encrusted by calcareous algae, are preferable for settling.

Embedding the shell in a trench is obviously of biological advantage for species of *Dendropoma* living in turbulent water, the snails anchored within the substrate are unlikely to be detached by waves.

## Aggregations

Vermetids tend to form aggregations, less common are species living solitary.

The individuals living solitary are not contiguous and there is a certain distance between them. The solitary vermetids are of considerable size, s.g. *Vermetus triqueter* 5-6 mm diameter (see pag. 171), *Serpulorbis arenaria* 11-15 mm diameter (B.D.D. 1884: 236), *Serpulorbis variabilis* up to 7-9 mm diameter (KAY, 1979: 108).

Aggregations may be loose or dense. The density being measured by number of individuals per unit of surface ( $n/cm^2$ ).

Loose aggregations, as well as solitary vermetids, are commonly found in calm waters protected from prolonged exposure.

In dense aggregations the crowded individuals are small and numerous.

They are closely apposed, entangled together, often forming extensive crust-like sheets over large areas, as *Dendropoma petraeum* on the (fig. 18) intertidal platforms in the Mediterranean Israel (TZUR and SAFRIEL, 1978: 124), and *Dendropoma gregaria* at Diamond Head Hawaii (HOPPER, 1982: 341).

Dense aggregations seem to be common in turbulent water, species of *Dendropoma* occurring in the intertidal zone exposed to wave action.

The density even of the same species may be influenced by external factors, such as strength of wave. According to Hopper densities of *Dendropoma gregaria* increases moving seaward edge of the platform: 9-12 individuals per cm<sup>2</sup> (HOPPER, 1982: 344). Lower densities are found on the shoreward edge of the platform 1-5 per cm<sup>2</sup> (HOPPER, 1982: 341).

#### Examples of typical dense aggregations (\*)

Species	Authorities
<i>Dendropoma corallinaceum</i>	HUGHES, 1979 a: 249, fig. 4
<i>Dendropoma corrodens</i>	KEEN, 1961: 206
<i>Dendropoma gregaria</i>	HADFIELD et al., 1972: 82, fig. 1
<i>Dendropoma irregulare</i>	HUGHES, 1979a: 247
<i>Dendropoma maximum</i>	MASTELLER, 1979: 259
<i>Dendropoma petraeum</i>	SAFRIEL, 1974: 1114
<i>Petalocochus innumerabilis</i>	KEEN, 1971: 403, fig. 497
<i>Petalocochus montereyensis</i>	HADFIELD, 1970: 308, fig. 2

Life in dense aggregations is obviously of advantage in:

1. Competitive superiority by monopolization of the space over large areas, thus excluding competition of other sedentary animals for space on the substrate.
2. Better exploitation of food particles gathered collectively by numerous individuals.
3. Fertilization is more ensured, as the spermatophores liberated into sea water chance more to reach the females in the aggregation concentrated in the same habitat.

#### Vermetidae in reef formation

Several gregarious species of Vermetidae are important in process of formation of reefs in warm waters. Such reefs occur in the Mediterranean and in some warm Atlantic shores. From the Mediterranean coast of Israel (Shiqmona, south of Haifa) such reefs were recorded by SAFRIEL (1966, 1975).

(\*) Dense aggregations of contiguous individuals were designed by HUGHES (1979) as « true colonies ». However the term « true colony » should be probably restricted to aggregations in which the individuals are bound together by live substance, built by asexual propagation as in sponges, bryozoans, tunicates (HADFIELD, pers. communication, 1982).

These reefs are situated in the intertidal zone on rocky platforms.

The raised edges of the platform margins are inhabited by dense aggregations of *Dendropoma petraeum* exposed to waves and surf swept.

The deeper internal part of the platform, where waters are relatively calm, protected from the full impact of waves, is inhabited by loosely aggregated *Vermetus triqueter*.

Intertidal reefs of vermetids similar to those of Israel are found in Lebanon and are also distributed elsewhere along the eastern part of the Mediterranean (SAFRIEL, 1975: 91).

Reefs on the same latitude as in Israel (32° 49' N, 34) are found in Bermuda (Atlantic). The sea surface temperature in summer is the same in both places (28°C). The reef forming species in Bermuda is *Dendropoma irregulare*.

Intertidal vermetid reefs are known also from Cape Verde Is., and Brazil (SAFRIEL, 1974: 1116).

#### List of species considered in this work (\*)

Authorities	Abbreviations
BANDEL K., 1976	(B)
HADFIELD et al., 1972	(Hd)
HUGHES R. N., 1978 a & pers. comm.	(Hu)
HUGHES R. N., 1978 b	(Hu)b
KEEN M., 1961	(K)a
KEEN M., 1971	(K)b
LIPKIN & SAFRIEL, 1971	(L.S.)
MORTON J. E., 1965	(M)
PRIOLO O., 1956	(P)
SCHEUWIMMER A. & NISHIWAKI S., 1982	(SN)

(\*) The specific adjectives (masculine or feminine) are given in the list according to the authorities cited.

<i>Vermetus adansonii</i> DAUDIN, 1800	West Africa, esp. Senegal (K)a
<i>Vermetus alii</i> HADFIELD & KAY, 1972	Hawaii Is. (Hd)
<i>Vermetus regulosus</i> MONTEROSATO, 1878	Mediterranean (P)
<i>Vermetus triqueter</i> BIVONA-BERNARDI, 1832	Mediterranean (M)
<i>Serpulorbis aotearoicus</i> MORTON, 1951	New-Zealand (M)
<i>Serpulorbis arenaria</i> (LINNAEUS, 1758)	Mediterranean (K)a
= <i>Vermetus gigas</i> BIVONA-BERNARDI, 1832	
<i>Serpulorbis aureus</i> HUGHES, 1978	South Africa (Hu)a
<i>Serpulorbis horrida</i> (MONTEROSATO, 1892)	Mediterranean (P)
<i>Serpulorbis imbricata</i> (DUNKER, 1860)	Japan (K)a
<i>Serpulorbis inopertus</i> (RUPPELL, 1830)	Red Sea (K)a
<i>Serpulorbis natalensis</i> (MÖRCH, 1862)	South Africa (Hu)b
<i>Serpulorbis novaehollandiae</i> (CHENU, 1843)	Australia (K)a
<i>Serpulorbis squamigerus</i> (CARPENTER, 1857)	California (M)
<i>Serpulorbis variabilis</i> HADFIELD & KAY, 1972	Hawaii Is. (Hd)
<i>Serpulorbis zelandicus</i> (QUOY & GAIMARD, 1834)	New Zealand (M)
<i>Tripsycha tulipa</i> (CHENU, 1843)	Panama (K)b
<i>Petalococonchus erectus</i> DALL, 1888	Caribbean Sea (B)
<i>Petalococonchus glomeratus</i> (LINNAEUS, 1758)	Mediterranean (K)a
<i>Petalococonchus innumerabilis</i> PILSBRY & OLSSON, 1935	West America (K)a
<i>Serpulorbis medusae</i> (PILSBRY, 1891)	Japan (SN)
<i>Serpulorbis daidai</i> SCHEUWIMMER & NISHIWAK, 1982	Japan (SN)
<i>Petalococonchus keenae</i> HADFIELD & KAY, 1972	Hawaii Is. (Hd)
<i>Petalococonchus macrophragma</i> CARPENTER, 1857	West Mexico (K)a
<i>Petalococonchus mcgintyi</i> OLSSON & HARBISON, 1953	Caribbean Sea (B)
<i>Petalococonchus montereyensis</i> (DALL, 1919)	California (K)a
<i>Petalococonchus nigricans</i> (DALL, 1919)	Florida (K)a
<i>Petalococonchus varians</i> ORBIGNY, 1841	Western Atlantic (K)a
<i>Dendropoma anguliferum</i> (MONTEROSATO, 1888)	Mediterranean (L.S.)
<i>Dendropoma corallinaceum</i> (TOMLIN, 1939)	South Africa (K)a
<i>Dendropoma corrodens</i> (ORBIGNY, 1842)	Caribbean Sea (K)a
<i>Dendropoma gregaria</i> HADFIELD & KAY, 1972	Hawaii Is. (Hd)
<i>Dendropoma irregulare</i> (ORBIGNY, 1842)	Caribbean Sea (K)a
<i>Dendropoma lamellosum</i> (HUTTON, 1873)	New Zealand (M)
<i>Dendropoma lituella</i> (MÖRCH, 1861)	California (M)
<i>Dendropoma maximum</i> (SOWERBY, 1825)	Red Sea (E. Indies) (K)a
<i>Dendropoma marchadi</i> KEEN & MORTON, 1960	East Africa (M)
<i>Dendropoma meroclista</i> HADFIELD & KAY, 1972	Hawaii Is. (Hd)
<i>Dendropoma petraeum</i> (MONTEROSATO, 1884)	Mediterranean (K)a
<i>Dendropoma platypus</i> MÖRCH, 1861	Hawaii Is. (K)a
<i>Dendropoma psarocephala</i> HADFIELD & KAY, 1972	Hawaii Is. (Hd)
<i>Dendropoma rhysoconcha</i> HADFIELD & KAY, 1972	Hawaii Is. (Hd)
<i>Dendropoma tholia</i> KEEN & MORTON, 1960	Mozambique (East Africa) (M)

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## REFERENCES CITED

- ABBOTT R.T., 1974 - American Sea Shells. Van Nostrand Reinhold Company, 663 pp.
- BANDEL K., 1975 - Das Embryonalgehäuse mariner Prosobranchier der Region von Banyuls-sur-Mer. *Vie Milieu*, **25** (1): 83-118.
- BANDEL K., 1976 - Observations on Spawn, Embryonic Development and Ecology of some Caribbean Lower Mesogastropoda (Mollusca). *The Veliger*, **18** (3): 249-271.
- BARNARD K.H., 1963 - Contributions to the Knowledge of South African Marine Mollusca, part III, Gastropoda: Prosobranchiata: Taenioglossa. *An. South Africa Museum*: 144-152.
- CURTIS L.A. and HURD L.E., 1981 - Crystalline style cycling in *Ilyanassa obsoleta* (Say). *The Veliger*, **24** (2): 91-96.
- FIORONI P., 1970 - Umwegige Entwicklung. *Naturwissenschaftliche Rundschau*, **23** (9): 352-360.
- FIORONI P., 1982 - Entwicklungstypen und Schlupfstadien bei Mollusken, einige allgemeine Befunde. *Malacologia*, **22** (1-2): 601-609.
- HABE T., 1953 - Studies on the eggs and larvae of the Japanese Gastropods (4). *Seto Marine Biological Laboratory*, **3** (2): 161-167.
- HADFIELD M.G., 1970 - Observations on the Anatomy and Biology of Two California Vermetid Gastropods. *The Veliger*, California, **12** (3): 301-309. Pl. 45,4 Text figs.
- HADFIELD M.G. et al., 1972 - The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. *Marine Biology*, **12**: 81-98.
- HADFIELD M.G. and C.N. Hopper, 1980. Ecological and Evolutionary Significance of Pelagic Spermatozoans of Vermetid Gastropods. *Marine Biology*, **57**: 315-325.



- HOPPER C.N., 1982 - The Ecology and Reproductive Biology of some Hawaiian Vermetid Gastropods. Thesis Ph. D., University of Hawaii, 379 pp.
- HUGHES R.N., 1978-a - A New Species of *Serpulorbis* (Gastropoda: Vermetidae) from South Africa. *The Veliger*, **20** (3): 288-291.
- HUGHES R.N., 1978-b - The biology of *Dendropoma corallinaceum* and *Serpulorbis natalensis*, two South African Vermetid Gastropods. *Journal of Linnean Society*, London, **64**: 111-127, 10 figs.
- HUGHES R.N., 1979-a - Coloniality in Vermetidae (Gastropoda. Systematic Association), *Adademic Press*, London. Special, **11**: 243-253.
- HUGHES R.N., 1979-b - Notes on the Reproduction Strategies of the South African Vermetid Gastropods *Dendropoma corallinaceum* and *Serpulorbis natalensis*. *The Veliger*, **21** (4): 423-427.
- HUGHES R.N. and LEWIS A.H., 1974 - On the spatial distribution, feeding and reproduction of the vermetid gastropod *Dendropoma maximum*. *J. Zool. London*. **172**: 531-547.
- HYMAN L.H., 1967 - The Invertebrates. Vol. VI, Mollusca I, 792 pp. 249 Text figs.
- IVANOV A.V., 1960 - Embranchement des Pogonophores, in *Traite de Zoology*, Ed. P. Grasse, Paris: 1523-1622.
- KAY A.A., 1979 - Hawaiian Marine Shells. *Bishop Museum Press, Honolulu*: 102-109, figs. 37-40.
- KEEN A.M., 1961 - A Proposed Reclassification of the Gastropod family Vermetidae. *Bulletin of The British Museum* (Natural History), Zoology, London, **7** (3): 181-213, Plates 54, 55; 33, Text figs.
- KEEN A.M., 1971 - Sea Shells of Tropical West America. Ed. II, Stanford Univ. Pres: 400-408
- KEMPF M. and LABOREL J., 1968 - Formation de Vermets et D'Algues Calcaires sur les cotes du Bresil. *Rec. Trav. St. Mar. End.*, **43** (59): 9-23.
- LIPKIN Y. and SAFRIEL U., 1971 - Intertidal zonation on rocky shores at Mikhmoret (Mediterranean, Israel). *J. Ecol.*, **59**: 1-30.
- LIVANOV N.A., 1949 - Polychaeta, in *Outlines of Zoology*, Vol. II, Invertebrata, ed. Dogel, Leningrad: 10-136.
- MACGINITIE G.E. and N. MACGINITIE, 1949 - Natural History of Marine Animals. Mac Graw Hill, N.Y.: 366-368.
- MASTALLER M., 1979 - Beiträge zur Faunistik und Ökologie der Mollusken und Echinodermen in den Korallenriffen bei Aqaba, Rotes Meer. Dissertation Ph. D., Bochum, 344 pp. 12 Text figs.
- MOERCH O.A.L., 1859-1860 - Etudes sur la famille des vermets. *J. Conchyliol*, **7** (4): 342-360; **8** (1): 27-48.
- MORTON E., 1951 - The structure and Adaptation of the New Zealand Vermetidae, part I. The genus *Serpulorbis*. *Transactions of the Royal Society of New Zealand*, **79** (1): 1-19, plates 1-3, 3 Text figs.
- MORTON J.E., 1955 - The Evolution of Vermetid Gastropods. *Pacif. Sci.* **9**: 3-15, 4 Text figs.
- MORTON J.E., 1965 - Form and Function in the Evolution of the Vermetidae. *Bull. Brit. Mus. (Nat. Hist.)*, London, **2** (9): 583-630.

- NORDSIECK F., 1968 - Die europäischen Meeres-Gehäuseschnecken (Prosobranchia) Von Eismeer bis Kapverden und Mittelmeer. Gustav Fischer Verlag, Stuttgart: 65-66.
- PRIOLO O., 1956 - Nuova revisione delle conchiglie marine di Sicilia. *Memoria* 9, Catania: 259-266.
- OWEN G., 1966 - Digestion, in *Physiology of Mollusca*, ed. K.M. Wilbur & Yonge C.M. Academic Press, New-York & London, Vol. II: 54-96.
- RUSSEL-HUNTER W.D., 1968 - *A Biology of Lower Invertebrates*. Mac. Millan Co. New-York: 128-131.
- SAFRIEL U., 1966 - Recent Vermetid Formation on the Mediterranean shores of Israel. *Proc. Malac. Soc.*, London, **37**: 27-34, 2 figs.
- SAFRIEL U., 1974 - Vermetid Gastropods and Intertidal reefs in Israel and Bermuda. *Science*, **186**: 1113-1116.
- SAFRIEL U., 1975 - The Role of Vermetid Gastropods in Formation of Mediterranean and Atlantic Reefs. *Oecologia* (Berl.), **20**: 85-101.
- SALVINI-PLAWEN L., 1981 - The Molluscan Digestive system in Evolution. *Malacologia*, **21** (1-2): 371-401.
- SCHEUWIMMER A., 1979 - Sperm Transfer in the Sessile Gastropod *Serpulorbis* (Prosobranchia: Vermetidae). *Marine Ecology*, **1**: 65-70, 6 Text figs.
- SCHEUWIMMER A. & NISHIWAKI S., 1982 - Comparative Studies on three Japanese species of *Serpulorbis* (Prosobranchia: Vermetidae) with Description of a New Species. *Venus*, **41** (2): 85-101.
- TZUR Y. and SAFRIEL U., 1978 - Vermetid Platforms as Indicators of Coastal Movements. *Israel Journal of Earth-Science*, **27**: 124-127.
- YONGE C.M., 1932 - Notes on feeding and digestion in *Pterocera* and *Vermetus*, With a discussion on the occurrence of the crystalline style in Gastropoda. *Sci. Repts. G. Barrier Reef Exped. Brit. Mus.* (Nat. Hist.), **1**: 259-281.

## Notes on Vermetidae in the Mediterranean waters of Israel

The Mediterranean coast of Israel is situated in the southern part of the Sea of Levant. The coastline is fairly straight, it extends at North Sinai in a narrow arc reaching the Suez Canal.

The northern part of the Israeli coast is dotted by rocky outcrops, whereas in the south sandy beaches prevail.

Tides are small and irregular in Israel, as in the Mediterranean in general, they range only about 25-30 cm. Changes of sea level often occur being effectuated by stormy winds and strong wave action.

The temperature of the water is in the Levant Sea almost tropical during the warmest period. In August the surface temperature rises to 25°-27°C, while in the rest of the Mediterranean it reaches only 20°-25°C.

The salinity is high in this part of South-Eastern Mediterranean, it reaches in Israel up to 38‰, and even 39‰.

The most prominent feature of the rocky section of Israeli coast are broad flat platforms, about 30-40 m across. Such platforms are rather uncommon in other parts of the world (SAFRIEL, 1974). The platforms are built of limestone and often covered by organic crust of vermetids (*Dendropoma petraeum*, *Vermetus triquetrus*).

The first records on Vermetidae in Israel were given by F. BODENHEIMER (1935) in « Animal life of Palestine ». Two species were mentioned there: *Vermetus glomeratus* and *Vermetus gigas*. G. HAAS recorded in « Prodromus Faunae Palaestinae » (1937, ed. Bodenheimer) 4 species: *Vermetus triquetrus* BIVONA, *V. glomeratus* L., *V. gigas* BIVONA and *V. horridus* MONTS.

CARMIN (1946) reported only *Serpulorbis arenaria*; AVNIMELECH & BOSKOWITZ (1955) recorded *Vermetus triquetrus*. In the publications of SAFRIEL (1966, 1974, 1975) and of LIPKIN & SAFRIEL (1971) were mentioned 5 species: *Vermetus triquetrus*, *V. regulosus*, *Serpulorbis arenarius*, *Dendropoma petraeum* and *D. anguliferum*.

In this paper 6 species of Vermetidae collected in the Mediterranean waters of Israel are treated, they were identified by M. KEEN (in litt., May 5, 1968).

Specimens belonging to these species are kept in the collections of the Hebrew University, Jerusalem and in the Tel-Aviv University.

### 1. *Vermetus (Vermetus) triquetrus* BIVONA-BERNARDI, 1832

Found in the intertidal zone: midlittoral and infra-littoral fringe, fixed to hard substrate. Mostly sheltered from surf, in rock pools, basins of platforms, where the agitation of water is negligible.

Solitary or in loose aggregations (var. *gregaria*). Common.

The shell of *Vermetus triquetrus* has an angulate circular aperture, diameter 5-6 mm.

Operculum small (less than half the diameter of aperture).

Predominantly mucous feeders.

Egg capsules (4-6) attached to the roof the female shell. Juveniles hatch in crawling stage, occasionally as veliconcha.

Distribution: Eastern Mediterranean, Western Mediterranean and Eastern Atlantic.

2. *Vermetus (Vermetus) rugulosus* MONTEROSATO, 1878

Found in the intertidal zone attached to rocks. Rare.

*Vermetus rugulosus* is endemic in the Mediterranean.

Distribution: Levant Sea and Western Mediterranean.

3. *Petalconchus (Macrophragma) glomeratus* (LINNAEUS, 1758)

Found in the intertidal zone (infralittoral fringe). Mostly solitary. Moderately common.

Shell small or moderately large, diameter of aperture 2-3 mm.

The last whorl unwound, free, medial whorls with two spiral laminae (calcareous plates projecting from the upper wall). Operculum smaller than aperture.

Distribution: Eastern Mediterranean, Western Mediterranean and Eastern Atlantic.

4. *Serpulorbis (Serpulorbis) arenaria* (LINNAEUS, 1758)

Found in the intertidal zone and infralittoral zone attached to rocks and stones, usually in calm waters. Solitary or in groups of 2-3 individuals. Very common.

Largest vermetids of the Mediterranean. Diameter of aperture 11-15 mm, operculum lacking. Mucous feeders.

Distribution: Eastern Mediterranean, Western Mediterranean, Eastern Atlantic.

5. *Dendropoma anguliferum* (MONTEROSATO, 1878)

Found in the intertidal zone (midlittoral and infralittoral fringe). Live in colonies. Rare.

The margin of aperture angulate with a keel on the external surface.

Operculum as wide as aperture. The colonies form dense aggregations.

Individuals corrodng trenches in the substrate.

Distribution: Eastern and Western Mediterranean. Endemic in the Mediterranean.

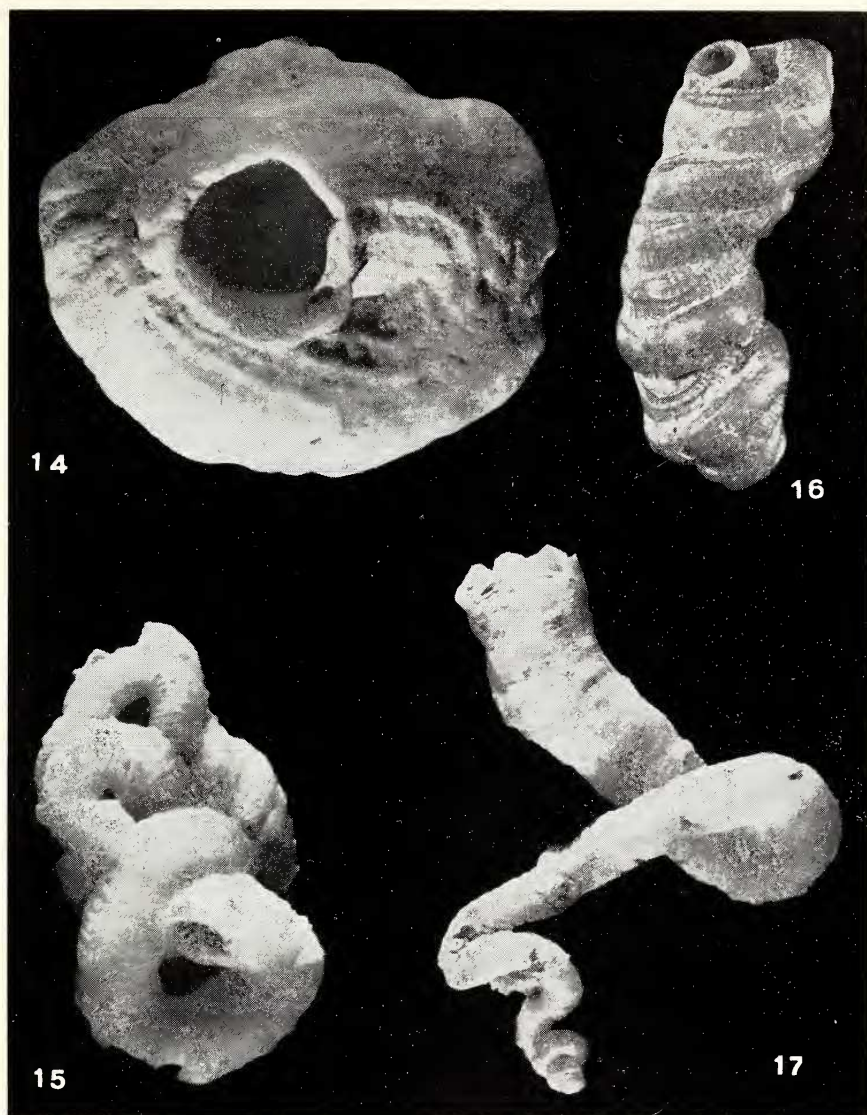


Fig. 14 - *Vermetus triqueter*.

Fig. 15 - *Vermetus rugulosus*.

Fig. 16 - *Petalconchus glomeratus*.

Fig. 17 - *Serpulorbis arenaria*.

6. *Dendropoma (Novastoa) petraeum* (MONTEROSATO, 1884)

Intertidal zone (midlittoral) on rocks exposed to wave action.

Live in dense aggregations on rocks. Common.

The shell relatively short, the lower part embedded in a trench corroded in the substrate.

The diameter of aperture 3-4 mm. The operculum as wide as the aperture. The aggregations in form of honey-comb-like sheets encrusting rocks.

Distribution: Eastern Mediterranean, Western Mediterranean and Eastern Atlantic (Portugal).

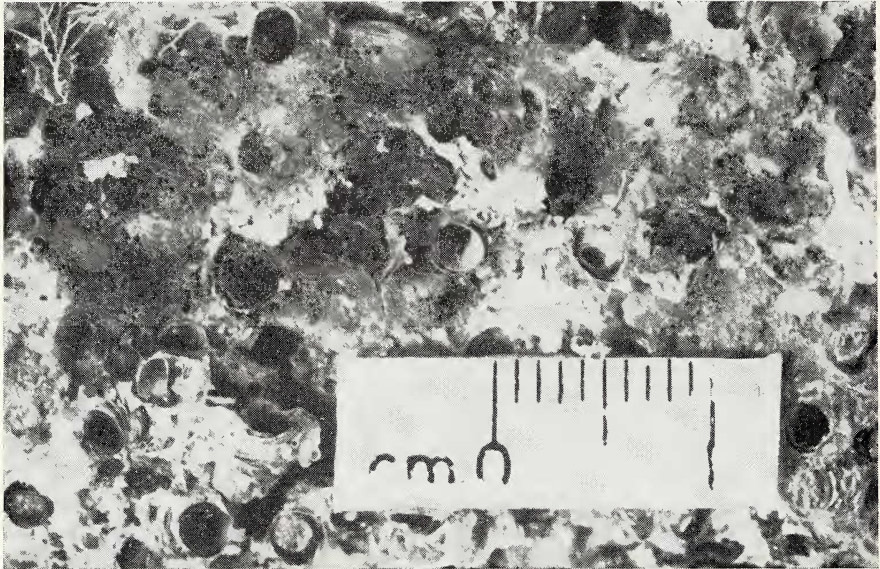


Fig. 18 - *Dendropoma petraeum*.

### General remarks

The Israeli species mentioned above exemplify the important characters of the family Vermetidae dealt with in the chapter «Structural and Biological adaptations of Vermetidae».

The vermetids as rock dwellers are concentrated at the northern part of the Israeli coast. In this area rocky shores with plentiful vegetation extend for long stretches and many species of invertebrates are living there. The small food particles required for the sedentary microphageous vermetids are abundantly available there.

Live specimens of all species were found in the intertidal zone, only *Serpulorbis arenarius* was found also in the infralittoral zone.

The 6 species of Vermetidae in the Mediterranean waters of Israel represent the main 4 genera of the family: *Vermetus*, *Serpulorbis*, *Petalconchus* and *Dendropoma*.

MONTEROSATO (1892) recorded as many as 18 species in of Vermetidae in the Mediterranean. However NORDSIECK (1968) listed only 8 Mediterranean species of vermetids, of them 6 are known from Israel. Their occurrence there was affirmed by M. KEEN (pers. commun., 1968).

In comparison with the number of vermetids in other areas is that of the rather short coastline of Israel (about 250 km) not scant.

From Hawaii were recorded 9 species (KAY, 1979); from the extensive area of Tropical West America - 13 species (KEEN, 1971) and from South Africa - 11 species (BARNARD, 1963).

Among the vermetids of Israel the following two species are, to our knowledge, predominantly mucous feeders: *Vermetus triqueter* and *Serpulorbis arenaria*. *Dendropoma petraeum* is a predominantly ciliary feeder. *Petalococonchus glomeratus* is feeding probably by the two means, both mucous and ciliary.

It is known that the female of *Vermetus triqueter* attaches her egg capsules to the roof of the shell. The larvae hatch mostly in crawling stage and sometimes as veliconcha (BANDEL, 1975: 89, 90).

As to the other Israeli species there is no sufficient information concerning the mode of their brooding and development.

The vermetid species known from Israel are concentrated in the Mediterranean and in areas close to this region. Noteworthy is the absence of all these species in the Black Sea, most of them are absent also in the Sea of Marmara, only *Vermetus triqueter* and *Serpulorbis arenaria* are found there. The absence of the species in these seas are obviously due to the particular ecological conditions in them (BARASH & DANIN, 1982: 98).

#### Regional Distribution of the Mediterranean vermetids of Israel

Species	Eastern Mediterranean			Western Mediter.	Eastern Atlantic.
	Levant Sea	Aegean Sea	Sea of Marmara		Ibero-Mor-roca region
<i>Vermetus triqueter</i>	+	+	+	+	+
<i>Vermetus rugulosus</i>	+	—	—	+	—
<i>Petalococonchus glomeratus</i>	+	+	—	+	+
<i>Serpulorbis arenaria</i>	+	+	+	+	+
<i>Dendropoma petraeum</i>	+	+	—	+	+
<i>Dendropoma anguliferum</i>	+	—	—	+	—

Two species are endemic in the Mediterranean: *Vermetus rugulosus* and *Dendropoma anguliferum*. Four species are found outside the Mediterranean in the Eastern Atlantic, but only in the Ibero-Moroccan region adjacent to the straits of Gibraltar.

The ecological conditions of the warm temperate Mediterranean Sea and the region in the Eastern Atlantic closely connected with this sea seem to be favourable of the existence of Vermetidae there.

#### Israeli Mediterranean species of Vermetidae recorded by MONTEROSATO (1892)

Species	Named by Monterosato	Text pp.
<i>Vermetus triqueter</i>	<i>Vermetus (Bivonia) triqueter</i> , BIV.	26
<i>Vermetus rugulosus</i>	<i>Vermetus (? Petalococonchus) rugulosus</i> , MONTS.	22
<i>Petalococonchus glomeratus</i>	<i>Vermetus (? Petalococonchus) subcancellatus</i> , BIV.	18
<i>Serpulorbis arenaria</i>	<i>Vermetus (Serpulorbis) gigas</i> , BIV.	30
	<i>Vermetus (Serpulorbis) polyphragma</i> , SASSO	35
<i>Dendropoma anguliferum</i>	<i>Vermetus (Siphonium) anguliferus</i> , MONTS.	44

References to *Vermetidae* in the Mediterranean waters of Israel  
(in particular)

- AVNIMELECH M. and V. BOSKOVITZ, 1955 - Some problems of the present distribution of Molluscan shells on the Mediterranean coast of Israel. *Bull. Res. Council. Israel.*, **5-B**: 178-188.
- BANDEL K., 1975 - Das Embryonalgehäuse mariner Prosobranchier der Region von Banyuls-sur-Mer - *Vie Milieu*, **25** (1): 83-118.
- BARASH AL. and Z. DANIN, 1982 - Mediterranean Mollusca of Israel and Sinai: Composition and Distribution - *Israel Journal of Zoology*, **31**: 86-118.
- BARNARD K.H., 1963 - Contribution to the knowledge of South African Marine Mollusca. Gastropoda, Polyplacophora, Scaphopoda. *Ann. South African Mus.*, Cape Town, **47**, part I, II: 360 pp.
- BODENHEIMER F.S., 1935 - Animal Life in Palestine. Jerusalem, L. Meyer, 506 pp.
- CARMIN J., 1946 - Mollusca of Palestinian Shores. *Bull. Indep. Biol. Laboratories, Kfar Malal, Palestine*. **4** (4): 1-9.
- HAAS G., 1937 - Mollusca Marina in Prodrromus Faunae Palaestinae by F.S. Bodenheimer. *Mem. Inst. Egypte, Cairo*: 275-280.
- KAY E.A., 1979 - Hawaiian Marine Shells. Bishop Museum Press, Honolulu, Hawaii, 652 pp.
- KEEN A.M., 1961 - A proposed reclassification of the Gastropod family Vermetidae. *Bull. Brit. Mus. (Nat. Hist.)*, Zoology, London, **7** (31): 183-213.
- KEEN A.M., 1971 - Sea Shells of Tropical West America. Stanford Univ. Press, 1064 pp.
- LIPKIN and SAFRIEL U., 1971 - Intertidal zonation on rocky shores at Mikhmoret (Mediterranean, Israel). *J. Ecol.*, **59**: 1-30.
- MONTEROSATO A.T., 1892 - Monografia dei Vermeti del Mediterraneo. *Bull. Soc. malac. ital.*, **17** (1-3): 7-48, 7 pls.
- NORDSIECK F., 1968 - Die europaischen Meeres- Gehäuseschnecken (Prosobranchia) von Eismeer bis Kapverden und Mittelmeer. Gustav Fisher Verlag, Stuttgart, 273 pp.
- SAFRIEL U., 1966 - Recent Vermetid formation on the Mediterranean shores of Israel. *Pro. Malac. Soc.*, London, **37**: 27-34.
- SAFRIEL U., 1974 - Vermetid Gastropods and Intertidal reefs in Israel and Bermuda. *Science*, **186**: 1113-1116.
- SAFRIEL U., 1975 - The Role of Vermetid Gastropods in the Formation of Mediterranean and Atlantic Reefs. *Oecologia* (Berl.), **20**: 85-101, Springer Verlag.